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THE EFFECTS OF HATCH-ORDER AND GENDER ON THE BEHAVIOUR OF BURROWING OWLS (*Athene cunicularia*)

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**THE EFFECTS OF HATCH-ORDER AND GENDER ON THE BEHAVIOUR OF
BURROWING OWLS (*Athene cunicularia*)**

by

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ABSTRACT

Burrowing Owls (*Athene cunicularia*) have an asynchronous hatch: females begin incubating well before the last eggs are laid, which results in age, size and developmental differences among the members of a clutch. Mating monogamously, for rarely longer than a season, Burrowing Owls have different sex-based roles within a mating pair. Males are typically more territorial than females, and might thus be expected to be generally more aggressive. Males defend their burrows, mates and offspring from predators or competing males while females spend more time incubating and caring for their offspring. I examine the effects of an asynchronous hatch and gender on the behaviour of juvenile Burrowing Owls. Intraspecific interactions between individual owls were observed within an enclosure, in which captive-bred owls are held before release and the relative aggressiveness or submissiveness of each bird was determined during each interaction. The results indicate that although there appears to be an association between the gender and asynchronous hatch on the behaviour of Burrowing Owls there does not appear to be any association between the clutch size and hatch weight on their behaviour.

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INTRODUCTION

The Burrowing Owl (*Athene cunicularia*) is a small, ground-dwelling owl that ranges throughout the western part of the Americas, from south-central British Columbia and southern Alberta, Saskatchewan and Manitoba, through the midwestern United States and into Central and South America (Campbell et al. 1990; Wilkerson and Siegel 2011). They inhabit arid regions, such as grasslands, deserts and prairies, where they build their nests in abandoned burrows dug by mammals such as badgers (*Taxidea taxus*), ground squirrels (*Uroditellus richardsonii*), black-tailed prairie dogs (*Cynomys ludovicianus*), Mexican prairie dogs (*Cynomys mexicanus*), etc. (Ayma et al. 2016; Poulin et al. 2011; Ray et al. 2016). Because they rely on other species—some of which are endangered—to dig burrows that the owls can use for nesting, burrow availability is often the greatest factor limiting Burrowing Owl populations (Klute et al. 2003).

Due to various factors, many of which can be associated with human activity, Burrowing Owls are not as abundant as they once were (Conway and Macias-Duarte 2015; Poulin et al. 2011; Wellicome 1997). Populations have been declining drastically due to increased mortality, range contraction, and increased predation associated with habitat fragmentation, degradation, contamination and loss, etc. (Poulin et al. 2005; Wellicome et al. 2014; Wilkerson and Siegel 2011). In Canada alone, their range has contracted by 65% and their numbers have declined 6-14% per year since the 1990's, resulting in a loss of more than 90% of the Canadian population (Conway J. 2018; Wellicome et al. 2014). Conservation efforts have been implemented throughout their international range to minimize owl mortality and habitat alteration (Environment Canada 2012).

As largely short distance migrants, Burrowing Owls are protected under the *Migratory Bird Treaty Act* (MBTA 1918) which is binding in Canada, the United States and Mexico. However, further protection of the birds varies among the three countries. (Lincer et al. 2018; Poulin et al. 2011). In Canada, they are listed as an Endangered Species according to the *Species at Risk Act* (S.C. 2002, c. 29). Different conservation techniques, such as captive breeding projects, building of artificial burrows and creation of conservation reserves have been implemented to limit and reverse the decline in Burrowing Owl populations by re-establishing self-perpetuating populations or reinforcing existing populations (Environment Canada 2012; Wellicome 1997). By better

understanding the behaviour, physiology, feeding habits, migration patterns and distributions of these birds, conservation efforts can be established in a way that minimizes detrimental outcomes (Johnson et al. 2010).

In many animals, the offspring of a single reproductive event are hatched or are born over a short period of time. In others, however, including Burrowing Owls, this is not always the case (Poulin et al. 2011; Wellicome 2005). Burrowing Owl young typically hatch asynchronously, over an extended period of time, as a result of the fact that females begin incubating before the entire clutch is laid (Conway et al. 2011; Podlas and Richner 2013; Wellicome 2005). Asynchronous hatching results in developmental differences between the first and last hatched chicks of a clutch (Podlas and Richner 2013; Wellicome 2005). This often has a detrimental effect on later hatched chicks, as they are generally smaller and have reduced chances of survival (Conway et al. 2011; Nilsson and Svensson 1996; Podlas and Richner 2013). The larger the clutch, the greater the degree of hatching asynchrony (Conway et al. 2011).

Female Burrowing Owls lay clutches of 6 to 12 eggs over a period of 8 to 17 days (Poulin et al. 2011; Wellicome 2005). Incubation usually begins once about half of the clutch is laid, but varies depending on the clutch size and distribution (Poulin et al. 2011; Wellicome 2005). Incubation lasts for 17 to 32 days and the eggs hatch within 1 to 7 days of each other, over an average time period of 3.8 days (Conway et al. 2011; Wellicome 2005). The resulting developmental differences between the earlier and later hatched chicks of a clutch may result in behavioural variations in addition to the obvious size differences (Beissinger and Waltman 1991; Podlas and Richner 2013). Chicks that hatch earlier, which are presumably larger, may be more aggressive as their greater size offers an advantage when competing against their smaller clutch mates for access to food (Stier et al. 2015). Conversely, chicks that hatch later, and that are thus smaller, may be less aggressive when competing against the larger members of the clutch for food (Kim et al. 2010). These smaller chicks may behave less aggressively than their larger clutch mates as a result of them being unable to confront these larger opponents.

Burrowing Owls mate monogamously (Conway and Macias-Duarte 2015). However, pair bonds of owls are not permanent and last rarely longer than a season (Poulin et al. 2011). Female Burrowing Owls spend much of the time within or near their burrows where they care for the young (Poulin et al. 2011). In contrast, males spend much of the time outside of the burrow,

guarding their mates and young from predators and competing males (Herse 2016; Poulin et al. 2011). As such, male Burrowing Owls may tend to be more aggressive than females. Conversely, female Burrowing Owls may tend to be less aggressive than males as they do not have compete for access to mates.

This study will examine whether asynchronous hatch and/or sex have any effect on the behaviours of Burrowing Owls in a captive setting.

METHODS

Field site

At the BC Wildlife Park, in Kamloops BC, Burrowing Owls are bred and the young are raised in an aviary before being released into the wild (at one year of age) to establish or reinforce populations of owls throughout British Columbia, Canada and Washington, USA. Within the aviary, there is a large flight pen encircling a central research centre that contains the burrows where mating pairs establish their nests (Figure 1). The flight pen is 40 m long, 25 m wide and 3 m tall (Figure 1). Each mated pair nests in its own burrow, contained within a small pen measuring 4 m long, 2 m wide and 3 m tall (Figure 2). These small pens, located inside the larger circular flight pen, allow the burrows and associated Burrowing Owl pairs to be isolated from each other while the birds are laying eggs and raising their young. Once the chicks are six weeks of age, the pens that separate each burrow within the flight pen are opened to allow for interactions among both juvenile and mature individuals between and within the different clutches. Adjacent to the circular flight pen there are two separate flight pens. At six months of age, the juvenile owls are placed into these two flight pens, based on their sex, to prevent premature pair formation (Figure 3). The mature owls remain in the initial circular flight pen (Figure 1.).

In some burrows (4 in the year of my study), a camera is used to determine when the eggs within a clutch are laid and hatch. After laying, eggs are marked sequentially, using a Sharpie marker, to provide a record of laying and hatch order. After hatching, a series of coloured plastic bands are added to one or both legs of each chick to allow for individual identification. At six weeks of age, blood samples are taken and the plastic leg bands are replaced with metal ones, each of which has a unique combination of a letter and a two-digit number, on each of the chicks. These letter-number combinations are large enough to be seen from the opposite end of the flight pen when using

binoculars. The blood samples are used to determine the sex of each of the chicks using DNA analysis.



Figure 1. Experimental Burrowing Owl enclosure at the BC Wildlife Park.



Figure 2. Enclosed burrow locations within the aviary at the BC Wildlife Park.



Figure 3. Juvenile sex based flight pens at the BC Wildlife.

Monitoring intraspecific behaviour

I observed the Burrowing Owls during randomly determined time intervals, which occurred at different times of the day, on different days of the week and both before and after they were fed between August 2018 and November 2018. I recorded all intraspecific behaviours of all of the birds that I could identify based on their unique leg bands. I sat in corners of the pen where I could observe at least one half of the enclosure at one time. I spent 30 minutes in one corner that maximized my visibility of the flight pen. After 30 minutes, I would observe from the opposite corner of the flight pen for an additional 30 minutes. Once the juveniles were separated into the sex-based pens (at 6 months of age) I would then spend a total of 30 minutes in each of the two sex segregated enclosures. The sex segregation enclosures were small enough that I could sit at one end of the pen and identify each of the owls within the pen.

While observing the owls, I took notes on any interactions between individuals, identifying the birds that took part and describing the interaction (which bird initiated it, how the individuals involved reacted, how long the interaction lasted, the cause of the interaction if known, and the time during the observation period that the interaction took place).

Dominance status

Dominance status was assigned once observations were complete. Documented behaviours were analyzed to determine pairwise dominance interactions between birds. Dominance within an interaction was inferred when one of the individuals supplanted or chased the other, or when one individual within an interaction resisted a supplanting attack by another individual in such a way that the resister was clearly dominant. Submissiveness was inferred when one of the individuals within an interaction did not resist an attack or when chased, tried to escape.

Within pairwise dominance interactions, individuals that were dominant were given a dominance score of 1. In comparison, individuals that were submissive; were given a dominance score of 0. For example, if bird A chased bird B and in response bird B flew away, bird A would receive a dominance score of 1 while bird B would receive a dominance score of 0. Interactions that included a group of individuals were considered as separate pairwise interactions for all the individuals involved. For example, if bird A chased a group of birds including birds B, C and D, a dominance score would be assigned for each of the pairwise interactions. That is, bird A would acquire a

dominance score of 3—1 for each 3 of the birds it dominated while birds B, C and D would each receive a dominance score of 0.

The dominance status of an individual over an observation period was determined by accumulating all the dominance scores of an individual and dividing it by the number of pairwise interactions it was involved in over that observation period. Therefore, during an observation period, the closer the dominance status of an individual was to 1, the more aggressive that individual was during that period. Conversely, the closer an individual's dominance status was to 0 the more submissive that individual was. A dominance status of 0 could be achieved if an individual was not observed interacting with other individuals during that observation period or if it only behaved submissively during all the observed interactions.

Each 30 minute observation period was subdivided into two, 15-minute segments. Since the dominance status of an individual was the number of dominance interactions divided by the number of interactions, an individual could acquire a maximum dominance status of 1 over a 15-minute observation period. Therefore, an individual could acquire a dominance status score of 2 for each complete, 30 minute observation period. This would therefore accumulate to give a total dominance status that is more representative of the bird's dominant or aggressive nature throughout the observation period.

A “behaviour rating” represents the total dominance status of an individual over all observation periods and was used to compare the dominance of different individuals. A behaviour rating is the sum of all the dominance status scores acquired from each of the observation periods. The higher the behaviour rating, the more frequently that individual was observed behaving aggressively.

First, I wanted to know if there were differences in the behaviour of juvenile owls before and after their separation from the mature owls into sex-based pens. The differences in the behaviour ratings of the juvenile owls, before and after their separation, was tested for normality using a Ryan-Joiner Test and the data was found to be normally distributed (RJ = 0.996; $p = >0.100$). As the data was normally distributed and was not independent, I used a Paired T-Test to determine if there were differences in the behaviour of juvenile owls before and after their separation from the mature owls into sex-based pens.

I also compared the difference in behaviour of juvenile male and female owls after separation from the mature owls. The behaviour ratings of juvenile males and females was tested for normality using a Ryan Joiner Test (Females: $RJ = 0.970$; $p = >0.100$; Males: $RJ = 0.972$; $p = >0.100$) while the equality of variances was tested using an F-Test, assuming a normal distribution ($p = 0.054$). Since the data was found to follow a normal distribution and had equal variances, a 2-Sample T-Test with pooled variances was used.

I then compared the behaviour ratings of the first two and last two chicks to hatch in all clutches. Clutches where hatch order was not known were not included. I determined the mean behaviour ratings of the first two chicks to hatch and the last two chicks to hatch in each clutch. A Ryan Joiner Test was used to test for normality of the differences of behaviour between the first and last two chicks to hatch within all the clutches. Since the differences in the behaviour were found to be normally distributed ($RJ = 0.987$; $p = >0.100$), a Paired T-Test was used for this comparison.

A Paired T-Test was used to compare the behaviours of individuals that hatched in the first of a clutch to that of individuals hatching in the second half. Again, clutches where hatch order was not known were not included in this comparison. I determined the mean behaviour ratings for individuals in the first half of the clutch and similarly, the mean behaviour ratings for individuals hatching in the second half of all the clutches. I then tested the difference between these scores for normality using a Ryan-Joiner Test ($RJ = 0.945$ $p = >0.100$).

I examined whether the behaviour of birds, after they were separated from the mature owls, was related to their hatch weight. The hatch weight of each chick was considered to the nearest gram, and birds were grouped into categories of 6, 8, 10, 12 and 14 grams. The mean behaviour ratings of the birds in each weight group were compared. There are some issues with pseudoreplication in these data, since often there was more than one bird in each weight group from a single clutch. However, they were treated as independent in order to have large enough samples for comparison. The normality of the data was tested using a Ryan-Joiner Test (Chicks weighing 6 grams: $RJ = 0.988$; $p = >0.100$, chicks weighing 8 grams: $RJ = 0.968$; $p = >0.100$, chicks weighing 10 grams: $RJ = 0.968$; $p = >0.100$, chicks weighing 12 grams: $RJ = 1.000$; $p = >0.100$ and chicks weighing 14 grams: $RJ = 0.903$; $p = >0.100$), which showed that the data in all groups was normal. I then examined whether the variances were homogenous using a Bartlett's test. ($p = 0.840$). Due to the

fact the data followed a normal distribution and had equal variances, a one-way ANOVA was used to compare the dominance scores of birds in different weight classes.

Finally, I examined whether that was any correlation between hatch order and hatch weight. A Paired T-Test was used to determine whether there were any differences in mean hatch weights of the first two versus the last two chicks to hatch in all clutches and then of chicks hatched in the first vs. the second half of their clutches.

RESULTS

There was no difference in the behaviour of juvenile individuals before and after they were separated from the mature owls into sex-based pens ($T = -1.27$; $p = 0.211$), (Table 1).

Table 1. Descriptive statistics of the Paired T-Test showing the differences in the behaviour ratings of chicks before and after they were separated from the mature owls.

Sample	N	Mean	StDev	SE Mean
Behaviour rating of juveniles before separation	35	0.343	0.553	0.093
Behaviour rating of juveniles after separation	35	0.573	0.858	0.145

There was a significant difference in the behaviour of juvenile males compared to juvenile females after they were separated into the sex-based enclosures ($T = -3.10$; $p = 0.004$), (Table 2). These results indicate that males tend to behave more aggressively than females of the same age, while exposed to individuals of the same age and sex (Figure 4). Thus, male Burrowing Owls tend to have a greater frequency of aggressive or dominant behaviours compared to females of the same age.

Table 2. Descriptive statistics of the 2-Sample T-test showing the differences in the behaviour rating of male and female chicks after they were separated from the mature owls.

Sample	N	Mean	StDev	SE Mean
Behaviour rating of juvenile females	23	0.283	0.618	0.13
Behaviour rating of juvenile males	12	1.128	0.998	0.29

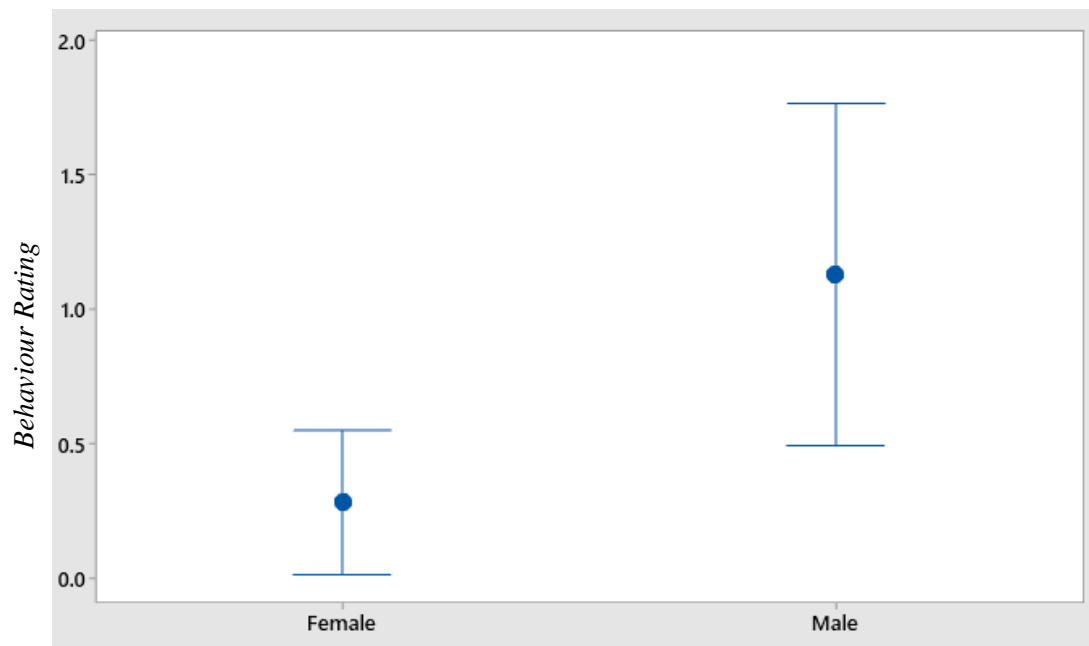


Figure 4. Interval plot of the behaviour rating of juvenile males and females. The dots indicate the mean and the interval bars show standard deviation.

There appeared to be no statistical difference in the behaviours of the first and last two chicks to hatch within a clutch ($T = 0.18$; $p = 0.872$), (Table 3).

Table 3. Differences in the behaviour rating of the first and last 2 chicks to hatch within a clutch.

Mean Behaviour Rating	N	Mean	StDev	SE Mean
First 2 chicks to hatch within all clutches	3	1.000	0.433	0.250
Last 2 chicks to hatch within all clutches	3	0.933	0.404	0.233

Since the asynchronous hatch seen in Burrowing Owls could result in behavioural differences among chicks within a clutch, I compared the behaviour ratings of chicks that hatched in the first half of each clutch to those in the second half of each clutch. It appears as though individuals that hatched in the first half of a clutch were more dominant than those that hatched in the second half of a clutch (T-Value = 5.68, $p = 0.005$), (Table 4, and Figure 5).

Table 4. Descriptive statistics of the differences in the behaviour rating of chicks depending on if they hatched in the first or second half of a clutch.

Mean Behaviour Rating	N	Mean	StDev	SE Mean
Chicks of 1 st half of all clutches to hatch	5	0.922	0.347	0.155
Chicks of 2 nd half of all clutches to hatch	5	0.350	0.418	0.187

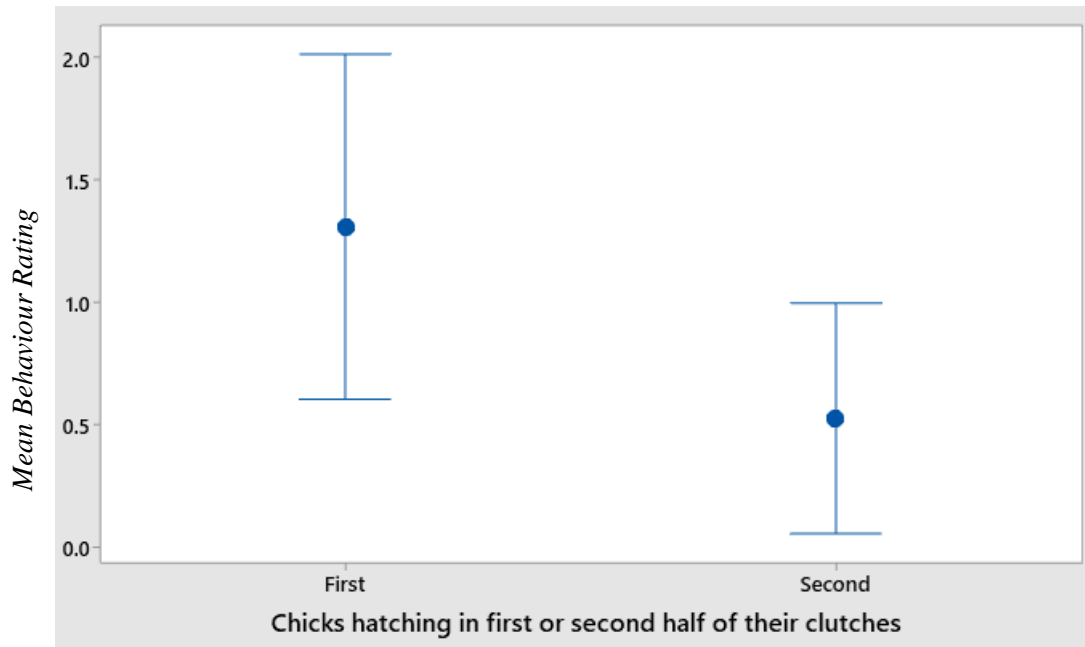


Figure 5. Interval plot of the mean behaviour rating of chicks based on whether they hatched in the first or second half of their clutches.

There were not enough samples to analyze the association between clutch size and behaviour. Therefore, I have simply examined the relationship graphically (Figure 6). As can be seen by Figure 6, the data does not appear to suggest that clutch size influences the behaviour of Burrowing Owls.

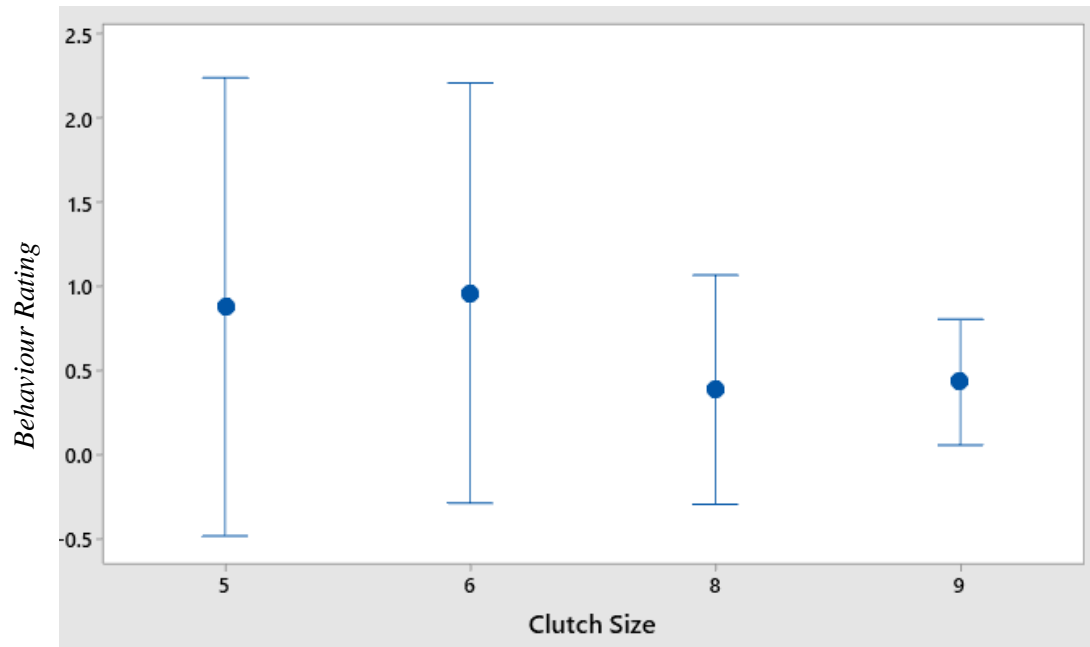


Figure 6. Interval plot of the total behaviour rating of chicks based on the number of eggs in a clutch.

The association between hatch weight and behaviour was tested using and a one-way ANOVA. It appears as though there is no significant association between the hatch weight of an individual and their behaviour, (F-Value = 0.41, $p = 0.800$), (Table 5).

Table 5. Association between hatch weight and behaviour.

Hatch Weight	N	Mean	StDev
6 grams	4	0.911	0.679
8 grams	10	0.600	0.810
10 grams	8	0.344	0.972
12 grams	2	0.925	0.955
14 grams	3	0.907	1.384

There was no significant difference between the average hatch weight of the first two chicks and the last to chicks to hatch in a clutch ($T = 0.945$, $p = 0.444$), (Table 6). Although the first birds to hatch were slightly heavier, the sample size was small.

Table 6. Descriptive statistics of the differences in the hatch weight of chicks depending on if they were the first or last 2 chicks to hatch in a clutch.

Mean Hatch weight	N	Mean	StDev
First 2 chicks to hatch within all clutches	3	9.667	14.333
Last 2 chicks to hatch within all clutches	3	8.000	1

There was also no significant difference in the average hatch weight of the chicks in the first half of a clutch compared to the average hatch weight of chicks that hatched in second half of the same clutch ($T = 0.915$, $p = 0.428$), (Table 7). Again, however, the sample size is small, and the average weight of chicks that hatched in the first half of a clutch was slightly greater than the average weight of those that hatched in the second half of the same clutch.

Table 7. Descriptive statistics of the differences in the hatch weight of chicks depending on if they hatched in the first or second half of a clutch.

Mean Hatch weight	N	Mean	StDev
Chicks in 1 st half of all clutches to hatch	4	9.3	6.76
Chicks in 2 nd half of all clutches to hatch	4	8.375	1.229

DISCUSSION

Within a mated pair, Burrowing Owls have different sex-based roles (Conway. 2018). Male Burrowing Owls are more territorial and seem to have an innate tendency to protect their mate, their chicks and their burrow from predators and competing males (Poulin et al. 2011). Conversely, females are involved primarily in brooding and so spend much of the time within their burrows (Kim et al. 2010). I thus hypothesized that juvenile males would behave more aggressively than females and the data confirms this.

Unlike many bird species, Burrowing Owls chicks hatch asynchronously (Lincer et al. 2018). That is, eggs that are laid and incubated earlier, also hatch earlier, which puts them at a developmental

advantage compared to their later laid and incubated clutch mates (Conway et al. 2011; Wellicome 2005). I hypothesized that the developmental differences that result from an asynchronous hatch would result in behavioural differences between the members of a clutch. Chicks that hatch earlier and that are presumably larger will be more aggressive than their later hatched and thus smaller clutch mates. It appears as though the asynchronous hatch as seen in Burrowing Owls is associated with differences in behaviour. The data indicates that chicks that hatched in the first half of their clutches tend to be more aggressive or dominant than those chicks that hatched in the second half of their clutch.

A greater degree of hatching asynchrony, the span of time between the first and last hatched members of a clutch, could be associated with greater variations in intraspecific behaviours (Conway et al. 2011). Increasing hatching asynchrony would result in greater age and size differences (Kim et al. 2010; Conway et al. 2011). It is possible that the increased hatching asynchrony could result in more pronounced behavioural adaptations within the members of a clutch (Wellicome 2005).

Additionally, it is possible that the environment in which the owls are raised could influence their behaviours (Gilby et al. 2013). Clutches that hatch in the wild are faced with greater food limitations than those raised in captivity, which have a constant supply of nutrient-rich food, such as was the case in this study. Food limitations during breeding, egg formation, egg laying and brooding could result in an even stronger association between, behaviour and hatching asynchrony. Asynchronous hatching in altricial birds, such as Burrowing Owls, is thought to be an adaptive response to unpredictable food availability as it facilitates the differential growth and survival of chicks (Skagen 2019). When food is limited in asynchronous clutches, the largest chicks grow faster than the smallest chicks, as the later hatching and thus smaller chicks are fed less than their older and larger clutch mates (Skagen 2019). Therefore, the increasing separation in size as a result of food limited situations, as would occur in wild population, could result in more polarizing behaviour.

Chicks born in a larger clutch would have to compete against more individuals for access to necessary resources required for development than those from smaller clutches (Wellicome 1997, Dijkstra et al. 1990). Additionally, individuals of a greater hatching weight would have a size advantage over their clutch mates and so would be able to access more food resources by

dominating their smaller clutch mates by behaving more aggressively (Podlas and Richner 2013). Chicks of lower hatching weight would have to behave more aggressively to compete against their larger clutch mates for access to food. Accordingly, I hypothesized that behaviour would be associated with both clutch size and hatch weight. However, it appeared as though the behaviour of the owls was independent of both clutch size and hatch weight. Again, this may be due to the fact that food was not limited in this captive environment.

Interestingly, the results suggest that hatch order does not appear to be associated with hatch weight; that is, chicks that hatch earlier in a clutch are not significantly larger than those that hatch later. Therefore, the increasing dominance or aggression seen in chicks that hatched among the first 2 or within the first half of their clutch was not simply, or definitively a result of their hatch weight. The increasing aggression seen in these earlier hatching chicks cannot be associated only with hatch weight and may therefore be associated with other phenomenon, such as simply age (time out the egg).

Overall, the results of this study suggest that there is no effect of clutch size or hatching weight on the behaviour of Burrowing Owls in captivity. However, there appeared to be a significant association between the behaviour of individuals and their gender, and early hatched chicks were more dominant than those that hatched later. The greatest limitation faced by the study was the fact that the birds were all captive raised. Therefore, an important continuation of this work would be to examine the effects of captivity on asynchronous hatch, clutch size and hatching weight; that is, how these factors vary between captive and wild young. As well as how these factors affect the behaviour of the owls in a wild environment.

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